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Opinion

Time to rethink trophic levels in aquaculture policy

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Abstract

Aquaculture policy often promotes production of low-trophic level species for sustainable industry growth. Yet, the application of the trophic level concept to aquaculture is complex, and its value for assessing sustainability is further complicated by continual reformulation of feeds. The majority of fed farmed fish and invertebrate species are produced using human-made compound feeds that can differ markedly from the diet of the same species in the wild and continue to change in composition. Using data on aquaculture feeds, we show that technical advances have substantially decreased the mean effective trophic level of farmed species, such as salmon (mean TL = 3.48 to 2.42) and tilapia (2.32 to 2.06), from 1995 to 2015. As farmed species diverge in effective trophic level from their wild counterparts, they are coalescing at a similar effective trophic level due to standardisation of feeds. This pattern blurs the interpretation of trophic level in aquaculture because it can no longer be viewed as a trait of the farmed species, but rather is a dynamic feature of the production system. Guidance based on wild trophic position or historical resource use is therefore misleading. Effective

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aquaculture policy needs to avoid overly simplistic sustainability indicators such as trophic level. Instead, employing empirically derived metrics based on the specific farmed properties of species groups, management techniques and advances in feed formulation will be crucial for achieving truly sustainable options for farmed seafood.

Key words: aquaculture, feed, policy, seafood, trophic level.

Introduction

The aquaculture sector accounts for half of all fish and seafood produced globally, provides an important source of nutrition in some of the world's most rapidly developing countries and will be key for meeting future global fish demand (Beveridge *et al.* 2013; Béné *et al.* 2016; Belton *et al.* 2018; Costello *et al.* 2020; FAO, 2020). Of the 80 million tonnes of food biomass produced by aquaculture, approximately 70% is sustained by human-made compound feeds (FAO, 2018). Among the ingredients used to formulate fish and invertebrate feeds, the fishmeal and oil used as protein and lipid sources have attracted considerable scrutiny because they are largely derived from wild-caught forage fish (e.g. anchovies, herring). The key role forage fish play in marine ecosystems has created concern over their extraction, and tension over the food security implications of diverting these nutritious species away from human consumption (Tacon & Metian, 2009; Siple *et al.* 2019). But at present, the high demand for these resources by the feed industry and favourable profit margins reduces incentives and innovation efforts for increasing direct consumption (Wijkström, 2009). The use of fishmeal and oil in aquafeeds has, therefore, cast doubt over the environmental sustainability of farming carnivorous taxa, such as salmon. Reducing the dependence of aquaculture feeds on wild-caught fish is widely recognised as an important strategy for the sustainable growth of aquaculture.

Environmental and supply chain concerns have led to widespread calls to refocus fish farming on low-trophic level species whose natural diets do not include fish. In natural food webs, the vast majority (~ 90% on average; range 80-95%) of the energy captured by primary producers is lost through energy expenditure (such as growth, reproduction, foraging, predation avoidance and other mechanisms) and only a small fraction passes to the trophic level above (Bonhommeau *et al.* 2013; Tucker & Rogers, 2014; Watson *et al.* 2014; Sanders *et al.* 2016). The inherent inefficiency of trophic transfers through food webs means that the higher the trophic level of an animal eaten by humans; the more ecosystem energy is embodied in its production. Recent reports from the World Resources Institute, World Wildlife Fund, Asia Pacific Fisheries Commission, and High-Level Group of Scientific Advisors to the European Union recognise this inefficiency, and advocate for farming and consuming 'fish low in the food-chain' to help achieve production and sustainability objectives for aquaculture (Waite *et al.* 2014; WWF, 2016; EU, 2017; FAO, 2017). In the United States, the 2019 Californian *Ocean Resiliency Act* (SB-69) now stipulates that coastal aquaculture permits should be focused on 'shellfish, seaweed and other low-trophic mariculture production' (Weiner et al. 2019). Thus, trophic level-oriented guidance (based on the natural trophic level of corresponding wild species) has begun to manifest in both governance and Best Practices guidelines for aquatic ecosystems.

Invoking labels from food web ecology assumes that the trophic level concept is readily applicable in an aquaculture setting, such that generalisations about trophic transfer efficiency enable us to equate low-trophic levels with greater sustainability. Yet 'low-trophic level' aquaculture production can take many forms – from unfed shellfish, seaweed and finfish (such as some filter-feeding carp species) to fed species that primarily depend on plant products in their feeds (Cao *et al.* 2015). Moreover, feeding practices, diets and production technologies have not been static through time. Continual reformulation of feeds is increasingly shifting the diets of farmed species away from that of their wild counterparts (Tacon & Metian, 2009, 2015; Kaushik & Troell, 2010), creating ambiguity in the interpretation of trophic level as a trait of the species being cultured. The premise of this study is that the complexity of designating trophic levels in aquaculture has unexamined implications for devising policy positions and Best Practices guidelines to enhance the sustainability of aquaculture.

To evaluate the meaning of trophic level for farmed seafoods, we use global aquaculture production, diet and feed efficiency data to calculate the effective trophic level of fed aquaculture species from 1995 to 2015. Our results elucidate three broad reasons why focusing on production of low-trophic level species may be unhelpful for increasing the sustainability of aquaculture. Looking forward, we discuss how clearer dialog and policy could support the responsible and sustainable use of feed ingredients for aquaculture production as the sector continues to grow and becomes more important for food security globally.

Aquafeed advances blur trophic position and taxonomic distinction

During early growth of the aquaculture industry in the 1980s and 1990s, fishmeal and oil were used heavily in

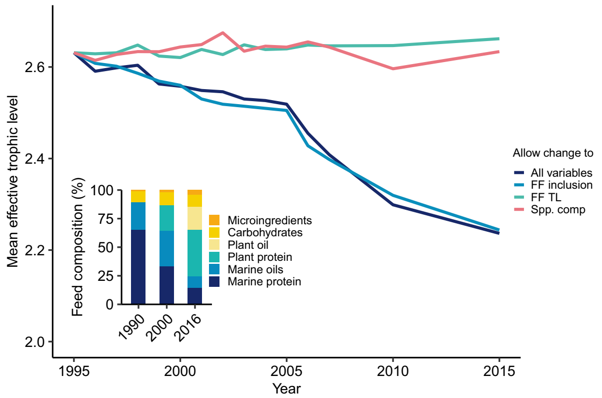

Figure 1 Temporal evolution of the mean effective trophic level of fed aquaculture. Sensitivity analysis of the mean trophic level change for global fed aquaculture over time since 1995. FF inclusion = only the observed forage fish inclusion rates are changed through time. FF TL = only the observed shifts in trophic level of wild-caught forage fish composition used for feed are changed through time; Spp. comp = only observed changes in the composition of farmed species are included. For each of these combinations, the other two variables were held at 1995 values. All variables = forage fish inclusion, forage fish trophic levels and species composition change with observed values through time. Inset picture shows the temporal change in Atlantic salmon diets in Norway from 1990 to 2016 taken from Aas *et al*. (2019) as an example of feed composition shifts.

aquafeeds as palatable, nutrient-dense and cheap sources of protein and lipids that matched the requirements of farmed fish (Turchini *et al*. 2019). For farmed carnivores, this meant feed composition closely resembled natural diets, dominated by fish-derived ingredients, but also included small amounts of plant–protein and oils (Fig. 1a). Conversely, feeds for naturally herbivorous species, such as carp and tilapia, were largely plant-based, but including fishmeal improved growth rates and body condition substantially (Tacon & Metian, 2008; Klinger & Naylor, 2012; Cao *et al*. 2015).

Stagnation in global catches of wild forage fish, competition from other economic sectors and the enormous expansion of aquaculture production over the past 30 years has driven substantial shifts in the formulation of aquaculture feeds as the price gap between fishmeal/oil and other ingredients widens (Turchini *et al*. 2009, 2019). Reduced dependence on marine ingredients has occurred with a greater shift towards crops such as soybean, canola, maize, wheat and nuts to supply energy, protein and oils for farmed taxa (Tacon *et al*. 2011; Troell *et al*. 2014; Pahlow *et al*. 2015; Fry *et al*. 2016). For example, feeds for Atlantic Salmon (*Salmo salar*) farmed in Norway have reduced total fish protein inclusion from 65% in 1990 to under 15% in 2016, largely by replacement with plant-based proteins, oils and carbohydrates (Fig. 1 inset; Aas *et al*. 2019). Such shifts in the feeds provided to carnivorous species have been possible due to advances in aquaculture nutrition, such as better understanding of the importance of supplementing diets with essential, conditionally essential and non-essential amino acids, and the effects of aquafeed processing on digestibility (Wu, 2014; Salze & Davis, 2015; Turchini *et al*. 2019). For non-obligate carnivores, such as carps or tilapias, lower or no fishmeal inputs align with natural dietary habits and are typically well tolerated (Hasan & New, 2013; Cottrell *et al*. 2020). Thus, there is now far greater representation of ingredients of trophic level 1 in feeds for multiple taxa.

Not only has the dietary profile of each fed aquatic species shifted through time, but also the overall species composition of farmed fish production has changed substantially at the same time that the actual trophic position of wild forage fish species used in feeds has varied dynamically. Taken together, these three factors have generated a substantial reduction in the effective trophic level of aggregate production of fed aquaculture: from 2.63 in 1995 to 2.23 in 2015 (Fig. 1, 'All variables'). If farmed fish diets and trophic levels of forage fish composition are instead held constant at 1995 values, we estimate that proportional changes to the species which are farmed would have resulted in very little change to the effective trophic level of fed aquaculture (Fig. 1, 'Spp. comp'; 2.631 in 1995 vs. 2.633 in 2015). When only the observed changes in the trophic level of species assigned as forage fish (and subsequently used in feeds) are accounted for, there is a very slight increase in effective trophic level through time (Fig. 1 'FF TL'). However, when only observed changes in the *amount* of fishmeal and oil included in feeds are accounted for through time (as opposed to the trophic level of fish used in feed ingredients), the mean effective trophic level responses of the fed sector closely track those that occur when observed shifts in all variables are accounted for (Fig. 1 'FF inclusion' vs 'All variables'). Thus, it is the reduced dependence on fishmeal and oil in feeds across farmed taxa that has overwhelmingly influenced the effective trophic level of fed aquaculture.

This shift in dietary composition means that most farmed taxa have been steadily diverging in effective trophic level from their wild counterparts. For most taxa, we estimate that average effective trophic levels of farmed animals were lower than median trophic levels of their wild equivalents even in 1995, and the difference has grown since (Fig. 2). The exceptions were freshwater crustaceans and tilapia which we estimate to have since decreased below median, although still within the interquartile range of, trophic levels of their wild counterparts (Fig. 2). Notably, we estimate that the effective trophic levels of other farmed freshwater finfish species (such as snakeheads, bass and perch) and anguillid eels have dropped from 3.33 and 3.53 to 2.64 and 2.81 respectively at a global level between 1995 and 2015. Marine fish and salmon have dropped an entire trophic level (3.38 and 3.48 to 2.43 and 2.42 respectively; Fig. 2). The net effect of temporal changes in feed formulation and alteration to the natural diet of cultured species is that many farmed taxa are now converging on effective trophic levels between 2.0 and 2.5 (Fig. 2). Thus, interspecific distinctions are becoming increasingly blurred: herbivorous fish are fed animal protein and thus farmed as omnivores, and carnivores have become omnivores as they are fed proportionally more plant proteins. This reality highlights the problem of characterising any particular taxon as 'unsustainable' based only on its wild or historic cultured trophic level. Instead, we must recognise different and dynamic inputs into feeds and the dynamic nature of practices and management used to grow them.

Trophic levels mask feed and resource efficiency

Focusing on trophic level as a metric of sustainability omits important aspects of resource efficiency. Through a combination of feed technologies, nutrition, selective breeding, feed and on-farm management practices, feed conversion ratios (the fraction of biomass eaten converted to new fish biomass) have, on average, improved (decreased) for all species globally (see distribution shifts on y-axis of Fig. 3). For some key species, like salmon, the improvements already have been substantial, though many other species have seen fewer improvements. This development has occurred in parallel with reductions in effective trophic level of these species in aquaculture (x-axis distributions Fig. 3), enabling carnivorous species, such as salmon – which we estimate to have dropped more than a whole trophic level since 1995 – to be more efficient than naturally herbivorous fish at converting feed into biomass when optimal ingredients are used (Fig. 3).

As average estimates, it is important to reiterate that the efficiency of individual production units will depend on feed resource qualities, specific management practices and environmental conditions. Feed conversion ratios do not take into account protein or nutrient retention – important aspects that reflect the capacity for aquaculture to efficiently deliver nutritional benefits to consumers (Fry *et al.* 2018). Further, it is true that, due to physiological differences in their digestive tracts, naturally herbivorous fish may be more efficient than carnivorous taxa in utilising low-grade plant material in feeds (Karasov & Douglas, 2013). Negative health and growth effects can result from replacing too much fishmeal and oil in feeds for carnivore species (Martin & Król, 2017; Krogdahl *et al.* 2020), although many can now be overcome through well-formulated feeds that supply an adequate balance of long-chain polyunsaturated fatty acids, vitamins, minerals and amino acids (Martin & Król, 2017; Turchini *et al.* 2019). Nonetheless, substantial research efforts on both optimisation of farmed carnivore species and of diets are ongoing (Caballero-Solares *et al.* 2018). Moreover, calls for low-trophic level production seem to neglect the fact that some carnivorous species retain certain key nutrients more efficiently than species of a lower trophic level (Fry *et al.* 2018).

Emphasis on the trophic levels of farmed species also biases our understanding of impacts of feeds in general. While there has been considerable attention paid to the sustainability implications of using relatively high trophic level ingredients derived from forage fish, these now comprise a relatively small proportion of modern feeds, and crops (trophic level = 1) now dominate feed composition across all aquaculture species (Pahlow *et al.* 2015; Tacon & Metian, 2015). But there has been a widespread lack of consideration for the consequences of displacing the burden of sourcing future aquafeeds from marine to terrestrial environments (Troell *et al.* 2014; Fry *et al.* 2016; Blanchard *et al.* 2017; Cottrell *et al.* 2018; Malcorps *et al.* 2019). Recent analyses have investigated global implications in terms of water and land use (Gephart *et al.* 2017; Froehlich *et al.* 2018b), but given that aquafeed ingredients are now tied to multiple food sectors, expansion of reliance on overstressed terrestrial agroecosystems and potential trade-offs across sectors need closer examination. The sustainability of terrestrial feed ingredients is only now being added as a consideration within the Aquaculture Stewardship Council certification standards, for instance (ASC, 2020).

Beyond neglecting other feed components, trophic level indices for farmed species fail to account for details of quality and sourcing of feed ingredients (Fry *et al.* 2018). For example, while wild-caught forage fish still provide the majority of fishmeal and oil used in fish and livestock feeds, a growing proportion is sourced from trimmings from farmed and wild-caught fish (FAO, 2018). Closing loops within feed sourcing processes in this way represents an important advance in resource efficiency. There could also be limitations if these waste streams represent lower quality ingredients or contamination vectors that influence the growth rates or nutritional composition of farmed taxa (FAO, 2018; FAO, 2020), leading to potential trade-offs from these seeming efficiency gains. These important sustainability considerations simply are not accounted for by trophic level classifications of aquaculture species.

Irrespective of how aquaculture develops, fishmeal and oil will almost certainly continue to be ingredients used for feed production in the short-term. As a multi-billion-dollar industry at the global level, forage fisheries are an important source of employment and livelihoods worldwide. Increasing demand for these ingredients has driven up their price in globalised commodity markets, but potential lower demand for fishmeal and oil for aquafeeds could relax competition with other sectors, such as terrestrial livestock and fertiliser (Froehlich *et al.* 2018a). In any case, aquaculture

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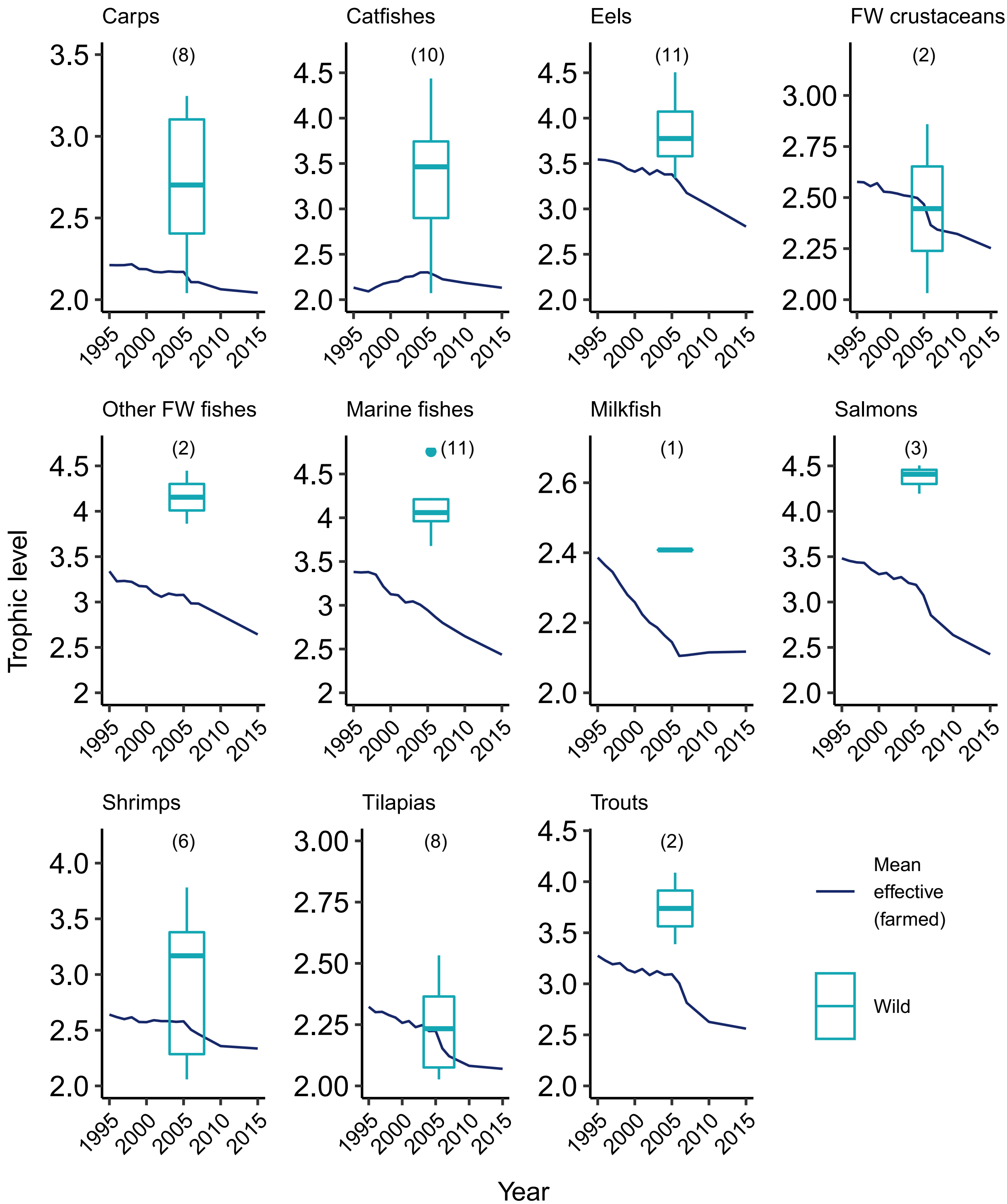

Figure 2 Temporal trends in global average farmed trophic levels across taxa relative to average reference values from wild counterparts. Note that y-axes have different maxima to effectively illustrate temporal trends *within* groups. FW = freshwater. Upper and lower boxplot hinges represent 75th and 25th percentiles respectively, and whiskers represent these quantiles plus or minus 1.5 times the interquartile range. Numbers in parentheses represent the number of species used to represent wild trophic levels within a taxon. Note trophic levels for wild species are not specific to any year.

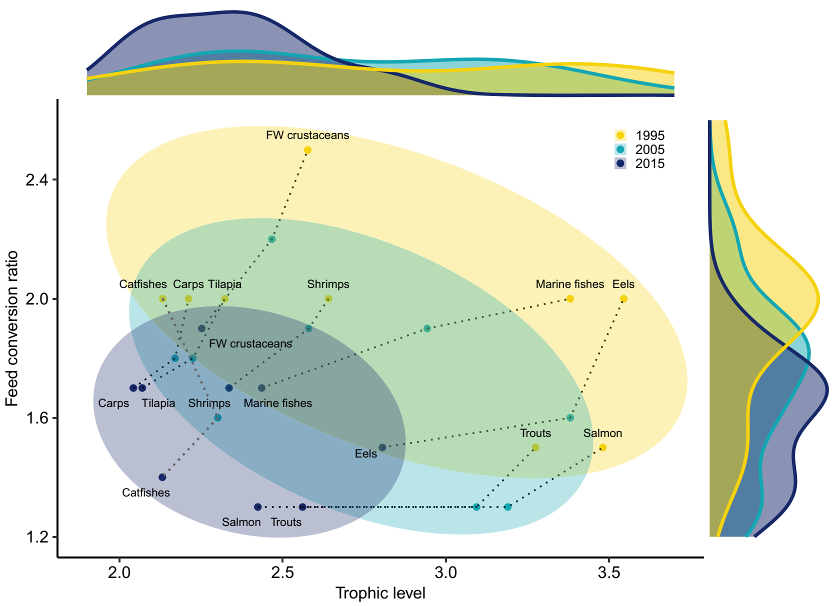

Figure 3 Temporal convergence of mean trophic levels and feed conversion ratios across major farmed taxonomic groups. Marginal density plots illustrate the distribution of trophic levels and feed conversion ratios on their respective axes for each year illustrated.

policy guidance should focus on the judicious use of forage fish as a limited resource rather than abstractions such as trophic levels of farmed seafood. A full evaluation of sustainability implications also must account for alternative uses for small pelagic forage fish, such as supporting the food and nutrition security of vulnerable human communities (Hicks *et al.* 2019) and maintaining a sufficient prey base for marine ecosystems (Siple *et al.* 2019).

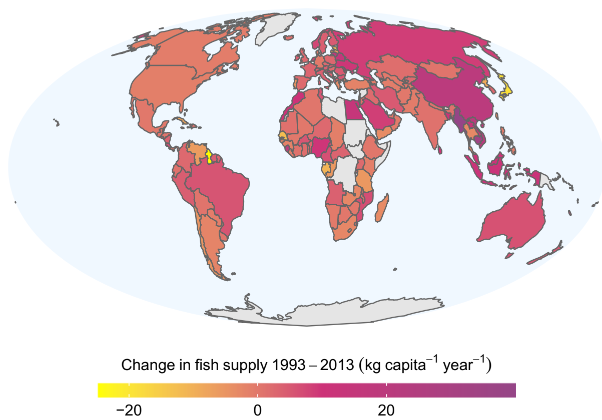

Figure 4 Change in apparent per capita fish consumption from 1993 to 2013. Apparent consumption is represented as per capita fish supply (the quantity available per person after production and imports are adjusted by exports, feed use and waste). NB: Fish supply data from FAO food balance sheets (FAO 2019) represents wet weight and not edible biomass. Grey fill = no data.

Growth in seafood demand will be accompanied by species-specific preferences

Critically, trophic level-oriented policies rarely address the tensions between the desire for improved environmental sustainability and growing global preferences for specific species. In China, for example, increasing consumer wealth is expected to substantially shift the nature of demand towards high-value species such as shrimp, lobster, salmonids and tuna, (World Bank, 2013; Fabinyi & Liu, 2014; Fabinyi *et al.* 2016), many of which can be farmed at the higher end of effective trophic levels. Many of these luxury items are scarce or perceived to be of lower quality in China (Crona *et al.* 2020), and with regulatory, spatial and environmental constraints set to pose limits on some future production, demand is increasingly likely to be met through imports (Crona *et al.* 2020), providing globalised production incentives. Global demand for these luxury products may increase further if the large increases in apparent fish consumption occurring in other rapidly developing and populous countries (e.g. Nigeria, Indonesia, Brazil; Fig. 4) are accompanied by shifts in preferences and buying power (Fig. 4). With high-value aquaculture dominated by private corporate entities, policies that focus on the trophic level of farmed species will be moot because they ignore the role of profit margins and demand growth in driving the trajectory of aquaculture under the current model of open-ended economic growth.

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Towards clearer aquaculture policy

The inferences and arguments presented above lead us to believe that dichotomous classification of 'low' or 'high' trophic level species in policy recommendations is unhelpful unless explicit recommendations are made. In many cases, unfed species, such as many bivalves and seaweeds, may provide considerably more environmental benefits with fewer environmental impacts than fed finfish (Chopin *et al.* 2001; Froehlich *et al.* ,2017, 2019). But these products serve different market sectors so their value as a reference point is, at best, context-dependent. If low-trophic level recommendations aim to increase production of finfish that are naturally non-carnivorous such as carp or tilapia, the sustainability of their dietary profile still needs to be considered and weighed against the efficiency with which they convert feed to edible and nutrient-rich biomass. For a given production unit, a species that is farmed at a higher trophic level because of greater proportions of dietary fishmeal/oil may still have a lower forage fish demand than less fish-dependent species if breeding, farming practices and feed manufacturing result in far superior feeding efficiency. Furthermore, feed ingredients other than forage fish have their own sustainability concerns, such as crops grown using environmentally damaging agricultural practices (Troell *et al.* 2014; Pahlow *et al.* 2015; Fry *et al.* 2016; Malcorps *et al.* 2019), even if their inclusion in feed results in a low effective trophic level of farmed production.

Trophic levels have been applied elsewhere for assessing the sustainability of fish and seafood. Temporal changes in the trophic level of wild capture fisheries catch have been used to understand how fishing has influenced marine ecosystems through time, for example, and can be applied as an indicator of exploitation or recovery (Pauly *et al.* 1998; Essington *et al.* 2006; Branch *et al.* 2010; Cao *et al.* 2017). In an aquaculture setting, trophic levels have been used to infer sustainability shifts for specific regions as production changes from mollusc to finfish farming (Stergiou *et al.* 2009; Tsikliras *et al.* 2014), yet such dynamics are primarily a reflection of market demand rather the sustainability of production practices per se. The aquaculture industry is highly motivated to adopt practices that improve efficiency of energy assimilation and the stability of feed supply chains, and continued gains can be expected from continued experimentation with feed composition and the genetics of farmed species. These developments will further undercut the value of trophic level as a measure of sustainability in aquaculture.

Trophic level indicators are attractive because of their simplicity and their familiarity from wider use in other disciplines, but the information embedded in these indices is insufficient for assessing the multiple facets of feed sustainability. Greater clarity in aquaculture policy regarding feed sustainability is within reach, however. Clear delineation between fed and unfed production practices are required. Where policy is aimed at encouraging unfed production, recommending bivalve molluscs, seaweed or filter-feeding fish based on environmental, social and economic considerations would add far greater specificity than trophic level stipulations. For the fed segment of aquaculture, continued changes in the formulation of compound feeds and convergence of effective trophic levels across taxa will trivialise the trophic levels of wild counterparts as a useful indicator of resource intensiveness. Instead, greater support for feed source transparency policies and participation in voluntary certification schemes, such as Aquaculture Stewardship Council (ASC), Best Aquaculture Practices (BAP) and Safe Feed/Safe Food (SF/SF) Certification Program in the US, should be embraced and incentivised.

Aquafeed production and tracing is notoriously challenging to quantify, is subject to high levels of uncertainty (Merican & Sanchez, 2016) and is rarely transparent. While numerous regulations around feed safety already exist (e.g. US Association of American Feed Control, Official Controls Regulation (EU) 2017/625), the source, and thus sustainability, of the feed is much less clear. On the certification side, the MarinTrust Standard (former IFFO RS) enables producers to select the most responsible sourcing options (from a fish stock management perspective) for raw marine feed materials (https://www.marin-trust.com/marintrust-standard). Further, the ASC has developed farm feed standards, that are unique in including both aquatic and terrestrial resources, that aim to minimise perverse social and environmental outcomes (ASC, 2020). Rather than concentrating on simple metrics of sustainability, these standards explore the nuance of supply chains, trade, and the factors that drive differences in social and ecological impact of production. Importantly, feed traceability policies or certification programmes equip governing bodies with the necessary tools for overseeing the growing aquaculture sector, while also empowering consumers and markets with the information needed to favour seafood products that are produced through best practices. Fundamentally, violation or adherence to an agreed set of standards that can be reassessed through time can provide policymakers with simple but effective metrics for regulation.

The dynamic nature of effective trophic level in fed aquaculture calls into question the use of trophic level as a trait of species grown and as a reliable indicator of sustainability. Naturally carnivorous and herbivorous species are both typically farmed as omnivores with converging effective trophic levels due to continued changes in feeding practices and formulation. While naturally herbivorous species can effectively utilise low-grade plant material for feeds, some carnivorous species may more efficiently convert feed into nutrient-rich biomass. But focusing on these different efficiencies does not necessarily result in a shift towards greater overall sustainability (Gephart *et al.* 2020). A world focused solely on efficiency of aquatic food – a world of 'aquatic chicken' – would favour globalised, vertically integrated seafood supply chains that would likely limit market access for marginalised communities and reduce the diversity of farmed products to a few key commodities. Thus, efficiency gains in one context may actually compromise the environmental and nutritional benefits of access to seafood for humanity as a whole (Gephart *et al.* 2020). Instead, a key goal of aquaculture development should be to create species-diverse and nutrient-diverse food sources that remain accessible and appropriate to people across regions and economies. Realising the potential of aquaculture to promote environmental sustainability requires integration of diverse goals, including food system stability, economic development and global equity. We have shown that trophic level classifications of cultured species can do little to guide us towards such a future because they ignore key intrinsic features of aquaculture production as well as broader macroeconomic and consumer demand. It is time to rethink the use of trophic levels in aquaculture policy.

Methods

We collated published data on aquaculture production, feed composition and trophic levels of wild fish species from a variety of sources to investigate temporal trends in the effective trophic level of fed aquaculture between 1995 and 2015. We also used food supply data to understand spatial changes in apparent human consumption of fish and seafood globally.

Data sources

We sourced all aquaculture production data from the United Nations' Food and Agriculture Organisation (FAO) production statistics using the FishStatJ statistical software, and fish supply data from the food balance sheets in the FAOSTAT statistics database (FAO, 2019). For data on aquafeed composition from 1995 to 2015, we used data from a number of published sources. We used fishmeal and oil proportions and feed conversion ratios from Tacon and Metian (,2008, 2015), the most comprehensive and internally standardised global dataset on typical feed use and efficiency across multiple taxa. We used data from Pahlow *et al.* (2015) for livestock by-product inclusion values for 2015, and given a lack of temporal data on by-product inclusion, we assumed that these ingredients increased exponentially to the levels used in 2015 to reflect an increasing rate of uptake typical of sigmoid adoption curves. (Rogers, 2003, Figure S1). A sensitivity analysis of linear versus exponential by-product inclusion and the associated influence on mean trophic levels of the fed sector is presented in Figure S2, although this makes no qualitative difference to the results. Salmons were the only exception to this rule as approximately 60% of global production occurs in the EU and Norway (Figure S3) where animal by-products are prohibited from use in feed. We therefore assigned a global value of 0% livestock by-product inclusion, although this had almost no influence on mean effective trophic level trends (Figure S2). For a detailed example of aquafeed composition change, we used data presented by Aas *et al.* (2019) on the shifts in composition of Norwegian Atlantic Salmon diets.

We extracted trophic level values for the wild equivalents of farmed species represented in our analyses using Fishbase and SeaLifebase repositories (Froese & Pauly, 2000; Palomares & Pauly, 2020). To capture the range of species represented in the broad taxa groups we use for effective trophic level calculations, we extracted available trophic level values from each database for the top ten species by farmed biomass within each taxon (or more if this did not represent more than 90% global production of that taxon). We conducted all analyses using R statistical software version 4.0.2. (R Core Team, 2020). All data and code used in this analysis are available at https://github.com/cottrellr/MTL_aquaculture.

Effective trophic level calculations

Effective trophic level calculations were required for both feed ingredients derived from forage fish (fishmeal and oil), and the farmed fish taxa. The mean trophic level of the fishmeal and oil used in feed largely depends on changes in the annual composition of the forage fish harvested to produce them. We therefore calculated the catch-weighted mean trophic level of forage fish using FAO landings data for major forage fish species harvested by render fisheries. Fish were assigned as forage fish using the same method as Froehlich *et al.* (2018). We selected species from the ISSCAAP 'marine fish' grouping, filtered by maximum size of 1200g, and extracted trophic level information according to species information in Fishbase (Froese & Pauly, 2000). Sorted by biomass, we calculated the mean trophic level of the all (n = 272) species using:

$$TL_{ff,i} = \frac{\sum_{1\rightarrow n}(prod_{1,i} \times TL_1) + (prod_{2,i} \times TL_2)\ldots + (prod_{n,i} \times TL_n)}{prod_{tot,i}} \quad (1)$$

where $TL_{ff,i}$ = trophic level of global forage fish in year *i*, $prod_{n,i}$ = production (landings) biomass of forage fish species *n* in year *i*, TL_n = reported trophic level of forage fish species *n, and* $prod_{tot,i}$ = the sum of $prod_{1\text{-}n}$ for in year *i*. The sensitivity of the mean trophic level of forage fish through time depending on species used is illustrated in Figure S4, but this does not change drastically when switching between all species or the top 20, 50 or 100 species (sorted by biomass). We recognise that at any given time the trophic level of fishmeal and oil provided in feed may be spatially variable as different forage fish species are randomly assigned for feed ingredients in different locations. But given the global nature of this analysis over a 20-year time span, we assume an even contribution of forage fish species to a 'pool' of fishmeal and oil. We assigned all livestock by-products included in feeds an invariant and conservative trophic level of 2.1 over the time period which is reflective of pig and poultry trophic levels and higher than that of ruminant meat (Bonhommeau *et al.* 2013). Proportional inclusion of crop ingredients in farmed fish diets was assumed to be the surplus unaccounted for by forage fish and livestock by-product ingredients (see Pahlow *et al.* 2015), and set to trophic level of 1. Using the trophic values assigned to feed ingredients, we calculated the annual global trophic level of fed aquaculture across 11 farmed taxa within the fed sector (carps, catfish, tilapias, milkfish, other freshwater fish, freshwater crustaceans, anguillid eels, trouts, salmons, shrimps and marine fish) and for the entire fed sector as a whole (marine crustaceans were omitted due to lack of temporal data in feed composition). We calculated annual individual taxon effective trophic levels as follows:

$$ETL_{x,i} = 1 + \sum\nolimits_{1\to f}\left(Prop_{1,i} \times TL_{1,i}\right) + \left(Prop_{2,i} \times TL_{2,i}\right)\ldots + \left(Prop_{f,i} \times TL_{f,i}\right) \quad (2)$$

where $ETL_{x,i}$ = effective trophic level of farmed taxon x in year i, $Prop_{f,i}$ = proportional inclusion of ingredient f in year i, $TL_{f,i}$ = trophic level of feed ingredient f in year i. These taxon level calculations were then used to create weighted averages of the trophic level of the global fed sector:

$$ETL_{fed,i} = \frac{\sum_{1\to f}(ETL_{1,i} \times prod_{1,i}) + (ETL_{2,i} \times prod_{2,i})\ldots + (ETL_{x,i} \times prod_{1,i})}{\sum_{1\to f}(prod_{1,i} + prod_{2,i} + \ldots prod_{x,i})} \quad (3)$$

where $ETL_{fed,i}$ = the effective trophic level of the global fed aquaculture sector in year i, $ETL_{x,i}$ = the effective trophic level of taxon x in year i, and $prod_{x,i}$ = production biomass of taxon x in year i. We then explored the main drivers of the temporal trends in global effective trophic level among; the proportion of fishmeal and oil included in feeds, the change in species composition of fed aquaculture, or the change in trophic level of forage fish used as feed using a sensitivity analysis. To explore the role of each variable, we held the values for the other two constant at 1995 values through time, while allowing the variable of interest to vary as observed, and study the effect on temporal trends in mean effective trophic level.

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Conflicts of interest

HEF is a member of the Technical Advisory Group for the Aquaculture Stewardship Council.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1 Assumed temporal change in animal by-product inclusion in aquafeeds for different cultured taxa through time.

Figure S2 Sensitivity analysis of using exponential or linear growth in animal by-product inclusion, or the inclusion in animal by-product in salmon feeds, on mean trophic level of the fed aquaculture sector.

Figure S3 Proportion of global production occurring in the EU and Norway across farmed taxa.

Figure S4 Temporal change in the mean trophic level of the major forage fish species used in render fisheries.